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Interindividual Behavioral Variability in Social Insects.—Robert L. Jeanne, ed. Westview Press, Boulder. 456 pp.

Westview Press is a leader in publishing timely and informative studies in insect biology. This volume provides novel insights into the topic of interindividual behavioral variability in social insects. Until recently, both the lay public and researchers alike thought of the social insect as an automaton. The "superorganism" concept of the social insect colony implied fixed roles for individuals, the colony's survival being paramount. Recent studies in kin and nestmate recognition have shown that social insects can discriminate among individuals and can also form dominance hierarchies.

Individual differences in behavior are currently best understood in primitively eusocial insects. However, all chapters but one in this volume deal with behavioral variability in highly eusocial insects such as ants and honey bees. In his introduction to this book, Jeanne states that it is not far-fetched to believe that no two social insect colony members behave alike during their lifetimes.

The first chapter, by Jaisson, Fresneau, and Lachaud, deals with individual traits of social behavior in ants. The methodological difficulties of studying individual social insects are discussed. One frequently used method is to isolate subjects for study. However, isolation itself may change behavior. The more widely used technique is marking and following individuals inside the colony.

The authors say that studies of social insects are either descriptive or experimental in nature. Descriptive studies use two possible recording methods. The first is the "sporadic sampling method," where behaviors are recorded at random. The second is the "systematic scanning method," where each behavior performed by each individual is recorded. The first method is good for estimating the number of behavior elements in the species. The second method is useful where there are fewer individuals and one wants to know how an individual behaves in the context of its society.

The authors give examples of the behavioral repertoires of *Pheidole, Leptothorax,* and *Zacryptocerus.* They point out that to a certain degree these repertoires are arbitrary since they depend on the criteria of the observer. It is therefore difficult to compare species using this kind of information.

Next there is a discussion of behavioral variability due to polymorphism (size castes) and age. An ethogram of *Pheidole hortensis* illustrates the different behaviors of minor and major workers. The authors then give an example of how social organization in *Ectatomma ruidum* was depicted using hierarchical cluster analysis and a dendrogram. They give examples from the literature of how social regulation can be studied by changing subcaste ratios, reducing the numbers of individuals in a colony, or removing a subcaste entirely.

The physiological correlates of individual behavior (such as ovarian development) are discussed next, followed by summaries of several studies on the ethogenesis of individual behavior. These studies deal with the role of individual experience during the young adult and larval stages. For example, if *Ectatomma* workers are isolated at emergence for 10 days and are then reintroduced to their colonies, they seemingly "regress' in behavior to day 1 individuals. They then normally develop into nurse ants.

The authors conclude that a "socially average" individual does not exist and that social insect colonies cannot be understood as just the average or sum of their members.

Harvester ants (*Pogonomyrmex barbatus*) like to keep their nests free of debris. Gordon used this trait to learn about the importance of the group context in role switching. By placing toothpicks on their mounds, she forced an increase in colony maintenance activity. She also interfered with foraging by putting barriers on their foraging trails. She wanted to know whether environmental changes that affect the numbers of workers doing one task also affect the numbers engaged in other tasks. She found that there is in fact interdependence of different tasks. Hence, understanding what an individual will do depends not only on its internal state and how workers doing some task respond to environmental changes, but also how workers doing some task respond to changes in the numbers doing other tasks. Understanding the individual's behavior cannot be understood without also understanding the dynamics of group behavior.

Calabi and Rosengaus, in a chapter on behavioral transitions in the ant *Camponotus,* used marked ants to show that, although the average responses of ants appear deterministic within age groups, individual workers show significant differences in the frequencies of behaviors. For example, although it is generally accepted that young workers care for brood, the authors found that 58% of their marked ants of known age never showed brood care. Indeed, given ants varied monthly in their proportionate frequencies of different behaviors despite constant colony conditions. This example of the use of transition probabilities will benefit readers unfamiliar with the technique.

Traniello's description of foraging behavior in *Formica schaufussi* also highlights individual variability. Workers can be classified as "persistent" or "non-persistent" foragers. The former do more area-restricted searches and generally leave and enter search sites at different angles. The latter do only limited area-restricted food searches and enter and leave the search area at the same angles. Using individually marked workers, the author shows that there is strong variation in how far workers travel and how long they are out of the nest, regardless of the success of their previous excursion. Thus, according to Traniello, workers vary in foraging "initiative" and thereby spatially partition their efforts.

His research shows that individual worker experience is also important and changes the persistence of foraging behavior in both types of workers. Sucrose rewards increase foraging persistence more than protein rewards (termites) in both types of workers, although the differences between the groups are still significant. If we assume that liquid carbohydrates are more likely to be persistent food sources than insects, then the workers are able to correlate their search duration with the type of food.

In the introduction to his study with *Leptothorax allardycei,* Cole points out that the superorganism concept of the social insect colony discouraged the search for individual differences. Kin selection theory, on the other hand, requires learning about individual behavior since we are interested in whether individuals receive differential treatment according to their relatedness. Reproductive competition among ant workers has received little attention. In *Leptothorax* the workers can reproduce and even have a dominance hierarchy among themselves that is correlated with their degree of ovarian development and the direction of food flow. Liquid food tends to go from lower- to higher-ranking individuals. The alpha worker is also nearer the eggs more often. Cole says that the superorganism concept is valid in cases where workers do not reproduce. Otherwise, there may be a conflict between a worker maximizing its own fitness and what is best for the colony as a whole. In the movement patterns of the workers, it is not possible to extrapolate from some "average" worker to explain nest behavior. Rather, colony order in this ant is involved with brood attraction and the agonistic interactions that form the dominance hierarchy. Colony efficiency may actually decline under these circumstances.

Carlin's report on dominance behavior among polygynous queens in the ant *Iridomyrmex purpureus* shows that dominance competition is evidenced by frequent bouts of mutual antennation in early stages of colony development. Mature colonies of this species can have more than one ovipositing queen, although they are in separate nest chambers and will fight if put together (this form of polygyny is called "oligogyny"). Carlin found that the dominance hierarchy begins upon emergence of the first workers 2.5 months after founding. The queens characteristically engage in bouts of mutual antennation lasting about 2 seconds, at an average rate of 30 times per hour for nearly a year. The bouts always end unambiguously with one of the queens backing or turning away. These bouts rarely involve biting. The queens do not eat each other's eggs. They begin to move apart after about a year, and are permanently separated after 23 months.

Before permanent separation, the queens occasionally reunite. Carlin found that the dominance ranking before the separation did not persist. Bouts of antennation were now longer. A queen that had won a recent bout was more likely to win the next bout. Oviposition during the bout increases the likelihood of winning for the subordinate queen and she lays more eggs than expected during these bouts. The queen's proximity to the egg pile is also important. Before separation, the dominant queen spent 81% of her time on the egg pile. During the reunions, both queens had a higher probability of winning if they were on the egg pile. The workers do not participate in queen dominance interactions. Carlin concludes that "hymenopteran colony politics is at least as intriguing as that of chimpanzees."

Rissing and Pollock also studied polygyny in an ant, *Veromessor pergandei.* Queens of this species co-found colonies. Pleometrosis can have several benefits, including rapid production of workers and a territorial advantage. The authors recently proved the latter using a test arena into which founding single- and multiple-queen colonies opened. Brood raiding was common among these colonies. In most cases (16/19) the multiple-queen colonies survived. Relatedness does not seem important in the queen associations, since queens collected at distant locations did just as well as those nearby in forming polygynous associations. After emergence of workers, most colonies reduce to monogyny, with many queens fighting to the death.

To survey the fate of polygynous queens in ants, the authors have tabulated what is known about monogyny and polygyny in ants. (I take exception to their suggestion that functional monogyny is best known in *Solenopsis invicta*—most fire ant researchers do not accept this interpretation.) In some species, once the advantages of queen mutualism are over, the queens eliminate one another. In other cases where oligogyny occurs, queen conflict is minimized. Furthermore, the authors state that, if workers show fidelity to their own queen or if there is restricted movement of workers among the various queens, the degree of relatedness between the queen and her workers rises. Such intra-colonial colony structures may make kin selection possible under these conditions.

Vander Meer, in his chapter on behavioral and biochemical variation in the fire ant, *Solenopsis invicta,* gives many examples of how ant biochemistry relates to their behavior and systematics. For example, major fire ant workers actually have less venom alkaloids than minor workers and are therefore not a soldier caste specialized for nest defense.

He has also looked at changes in responsiveness to pheromones. Brood-tending workers give the most consistent bioassay to a queen attractant, followed by reserves and foragers. Vander Meer concludes that the brood-tenders are the most "sensitive" (I prefer the term "responsive") to the attractant. They are also the most responsive to the trail pheromone. Since brood-tenders are young workers, Vander Meer suggests that senescence could account for the reduced responsiveness by the other workers.

In discussing nestmate recognition, Vander Meer distinguishes between endogenous (having a genetic component) and exogenous (environmentally derived) odors. It is still not known whether cuticular hydrocarbons are the recognition cues in ants. Individual colonies can be identified by their hydrocarbon pattern. However, the hydrocarbon make-up is dynamic, changing over time. Vander Meer says that the learning of nestmate odors must be an iterative learning process to allow for these changes.

Fewell's article on foraging behavior in the harvester ant *Pogonomyrmex occidentalis* indicates that workers either forage individually without trails or en masse on large trunk trails. He hypothesizes that habitat variation could explain the variability. He observed 15 colonies and determined the mean vegetational coverage around the nests. The foraging activity of the workers was then determined. Colonies surrounded by variable density vegetation (clear areas mixed with vegetation) usually had major trunk trails, while those surrounded by more even vegetation had more individual foraging. Ants in areas of low vegetation forage twice as far as those with high vegetation. Ants also form trunk trails in response to clumped resources (seeds). Thus, flexibility in colony foraging is dependent upon local resources. The author believes that foraging efficiency is improved with this strategy.

Post, Jeanne and Erickson present a comprehensive description of behavioral variability in *Polistes fuscatus variatus* based on data from 54 workers in 7 colonies. The first part of their article has a complete descriptive catalog of behavioral repertoires among workers (37 in all). They analyzed lifetime differences in these repertoires and age-related changes in behavior as well as individual variation in age polyethism and the frequency of giving food or pulp to nestmates.

The authors found that the behaviors are not performed at equal frequencies by all workers. Within each colony, workers can be categorized into one of three specialities: prey foragers, pulp and prey handlers, and non-foragers. These differences are quantitative rather than qualitative. Task partitioning by workers returning with prey is evident, workers turning over their booty to nestmates and then returning to the field. There is also evidence of age polyethism, although the only individual variation is the age at which the workers first leave the nest.

In the next chapter, Jeanne, Downing and Post discuss age polyethism and individual variation in *Polybia occidentalis,* an advanced eusocial wasp. The authors studied no less than 67 behavioral categories! Typical of many social insects, the young workers initially do building activities and change to foraging as they get older. The switchover is abrupt in some individuals, gradual in others. Individuals also differ in the age of their behavioral change.

There is also evidence of age polyethism with respect to foraging specialty, some workers foraging first for pulp and later for nectar. Not all workers show this trend. Furthermore, the typical eusocial pattern of worker specializations from in-nest, to on-nest, and finally off-nest phases, is not necessarily followed by all workers. Some rarely leave the colony during their entire lives. In those workers that progress from in-nest to on-nest tasks, the age of switching varies among individuals. If the colony were studied at the group level with "average" workers, we would see a gradual temporal change of behavior. However, when individuals are analyzed, the changes are more sudden. The authors say that in this species the order of roles is fixed, but not the absolute transition ages. They suggest age-dependent thresholds of responses to colony needs, with thresholds varying among workers.

"Undertaker" honey bees are the subject of Visscher's chapter. One inevitable consequence of social life is the need to dispose of the dead. The author found that an average of 54 dead bees/day were removed from each of 5 colonies, or about a liter a month of corpses. To study the responses of workers, Visscher placed freshly killed bees into hives. He built a trap that facilitated labeling bees that were removing corpses, and then found that some individuals remove corpses more often than expected by chance alone. He concluded that a specialized group of workers, comprising no more than 2% of the bees at any given time, is responsible for most of the undertaking. These bees have made their first orientation flights, but have not yet begun foraging. The author estimates that only 10% of all bees ever participate in this chore. He also did some tests to show that there is probably a chemical releaser for this necrophoric (undertaking) behavior.

Waddington's contribution to this book discusses the relationships between body size, individual behavior, and social behavior in honey bees. Larger bees begin new tasks earlier in life and also forage more frequently. The author measured 309 newly emerged bees and then counted the number of circuits in their waggle dance when they were signaling a food resource. The dance duration is known to be correlated with flight distance. For nectar collectors, there was no significant correlation between bee size and distance flown. On the other hand, there was a positive correlation with pollen collectors. In a second experiment, the author trained bees to food sources and also found a positive correlation between the bee's size and the distance to flowers.

Waddington states that proboscis length is related to body size in bees, so that different size bees can exploit different resources. He suggests that bee species that forage independently benefit from size variability since they can exploit a variety of resources. Species with recruitment to food, on the other hand, forage more efficiently if they have little size variation. The author tested these predictions using 11 species of stingless bees that vary widely in the complexity of their recruitment systems. In agreement with the predictions, he found a negative correlation between the size variance of the different species and the complexity of their recruitment system.

The final chapter in this book, by Plowright and Plowright, deals with "elitism" in social insects. By this the authors mean that some workers (the "elites") do much more work than others (the "loafers"). Why is this so? Do "reserves" constitute a back-up work force for emergencies? What are the causal mechanisms that account for these differences of behavior? Are the individuals genetically distinct or are the differences just probabilistic? The authors develop a positive feedback model of elitism, in which the successful completion of a task makes an individual more likely to repeat it ("internal" factors). The "external" factors in this model include the number of hungry larvae or state of food reserves in the colony. Using this model of worker behavior, the authors ran Monte Carlo simulations of social insect colonies. One of three general outcomes gave a bimodal distribution of time spent working, i.e., both elites and loafers were generated. This outcome does not prove that stochastic processes account for elitism, but that it is at least possible. The authors caution that many more ethological studies are needed to determine the relevant parameters for the development of elitism in real colonies. The simulations differ from real colonies in one important respect: if the model is run too long, the effects of the initial conditions are lost. In real colonies, on the other hand, elitism persists over time.

When I finished this book I was convinced that the study of individual differences in social insects has barely begun. Noticeably absent were any references to termites (hymenopterists seem to have a bias against working with them). Most social insect biologists will want a copy of this book in their libraries.—*Les Greenberg, Department of Entomology, Texas A&M University, College Station, Texas 77843.*